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Methane emission by alpaca and sheep fed on lucerne hay or grazed on pastures of perennial ryegrass/white clover or birdsfoot trefoil

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SUMMARY

Based on the knowledge that alpaca (*Lama pacos*) have a lower fractional outflow rate of feed particles (particulate FOR) from their forestomach than sheep (San Martin 1987), the current study measured methane (CH_4) production and other digestion parameters in these species in three successive experiments (1, 2 and 3): Experiment 1, lucerne hay fed indoors; Experiment 2, grazed on perennial ryegrass/white clover pasture (PRG/WC); and Experiment 3, grazed on birdsfoot trefoil (*Lotus corniculatus*) pasture (Lotus). Six male alpaca and six castrated Romney sheep were simultaneously and successively fed on the forages either *ad libitum* or at generous herbage allowances (grazing). CH_4 production (g/day) (using the sulphur hexafluoride tracer technique), voluntary feed intake (VFI), diet quality, and protozoa counts and volatile fatty acid concentrations in samples of forestomach contents were determined. In addition, feed digestibility, energy and nitrogen (N) balances and microbial N supply from the forestomach (using purine derivatives excretion) were measured in Experiment 1.

Diets selected by alpaca were of lower quality than those selected by sheep, and the voluntary gross energy intakes (GEI, MJ) per kg of liveweight$^{0·75}$ were consistently lower ($P<0·001$) for the alpaca than for the sheep (0·74 *v.* 1·36, 0·61 *v.* 1·32 and 0·77 *v.* 2·53 on lucerne hay, PRG/WC and Lotus, respectively). Alpaca and sheep did not differ ($P>0·05$) in their CH_4 yields (% GEI) when fed on lucerne hay (5·1 *v.* 4·7), but alpaca had a higher CH_4 yield when fed on PRG/WC (9·4 *v.* 7·5, $P<0·05$) and Lotus (6·4 *v.* 2·7, $P<0·001$). When grazing on Lotus, the sheep had very high protozoa counts in their forestomach contents, compared with those with the other forages and those in the alpaca. On lucerne hay and Lotus, but not on PRG/WC, the alpaca had higher ($P<0·01$) acetate/propionate ratio in their forestomach fluid than sheep. When fed on lucerne hay, alpaca and sheep did not differ ($P>0·05$) in diet N partition or microbial N yield, but alpaca had higher ($P<0·05$) neutral detergent fibre digestibility (0·478 *v.* 0·461) and lower ($P<0·01$) urinary energy losses (5·2 *v.* 5·8 % GEI) than sheep. It is suggested that differences between these species in forestomach particulate FOR might have been the underlying physiological mechanism responsible for the differences in CH_4 yield, although the between-species differences in VFI and diet quality also had a major effect on it.

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INTRODUCTION

Rumen particulate phase fractional outflow rate (particulate FOR) was a major contributor to the differences between individual sheep in methane (CH_4) yield (percentage of gross energy intake, % GEI) (Pinares-Patiño *et al.* 2003). Sheep with lower particulate FOR (i.e. longer retention times) had larger rumen fills and higher fibre digestibilities and CH_4 yields. Since the direct measurement of the particulate FOR and rumen fill is much more difficult under grazing conditions than under controlled conditions, the study of CH_4 production rates (per unit of intake) by species or breeds differing in these animal factors might reveal further insights into their involvement in CH_4 emission.

South American camelids (SAC: llama, *Lama glama*; alpaca, *L. pacos*; guanaco, *L. guanicoe*; and vicuña, *L. vicugna*) differ from sheep in the structure and function of their digestive system and therefore in their nutritional strategies (Vallenas *et al.* 1971; Heller *et al.* 1986; San Martin & Bryant 1989). Most comparative studies, under both penned and grazing conditions, have shown that SAC digest plant cell walls more efficiently than sheep (San Martin & Bryant 1989; Warmington *et al.* 1989; Dulphy *et al.* 1994, 1997; Lemosquet *et al.* 1996). This higher efficiency was attributed to a lower particulate FOR (San Martin & Bryant 1989; Dulphy *et al.* 1994, 1997; Lemosquet *et al.* 1996; Raggi & Ferrando 1998).

The study tested the hypothesis that alpaca and sheep, two animal species differing in particulate FOR from their forestomachs, would differ in their CH_4 emissions when fed three different forages: (a) lucerne hay fed indoors, (b) grazed perennial ryegrass/white clover pasture (PRG/WC) and (c) grazed birdsfoot trefoil pasture (Lotus).

MATERIALS AND METHODS

Experimental design

The study was carried out from October to December 1999 and involved three successive experiments (1, 2 and 3), each using a different forage. In each experiment, six alpaca and six sheep were each fed *ad libitum* (or generous pasture allowance when grazing) on the same forage at the same time.

Experiment 1 (indoors) was carried out at AgResearch Grasslands, Palmerston North, New Zealand, when chaffed lucerne (*Medicago sativa*) hay was fed. Experiment 1 comprised 15 days of acclimatization to the diet, followed by a 14-day period (days 1–14) for data and sample collection. Voluntary feed intake (VFI) was measured during the first 6 days of the collection period. Energy and nitrogen (N) balances, CH_4 production and microbial N supply from the forestomach were measured over days 7–12. Forestomach contents were sampled (by stomach tube) for protozoa count and analysis of volatile fatty acids (VFA, mol %) during the last 2 days of the collection period.

During Experiments 2 and 3 the animals were grazed on perennial ryegrass/white clover (*Lolium perenne*/*Trifolium repens*) pasture (hereafter named 'PRG/WC') and birdsfoot trefoil (*Lotus corniculatus* cv. Grasslands Goldie) pasture (hereafter named 'Lotus'), respectively, at Massey University, Palmerston North, New Zealand. Each of these experiments involved 15 days for acclimatization to the diet, followed by a 6-day period (days 1–6) for data and sample collection. Diet composition, feed intake and CH_4 production were measured during the first 4 days, after which, forestomach contents were sampled (by stomach tube) during 2 consecutive days for protozoa count and VFA analysis.

Animals

Six male alpaca of the Huacaya breed ($61{\cdot}4 \pm 10{\cdot}5$ kg; S.D.) and six castrated Romney sheep ($43{\cdot}0 \pm 1{\cdot}8$ kg; S.D.) were used. At the start of the study, the alpaca were 18 months old and the sheep 15 months old. All animals had been grazing perennial ryegrass/white clover pasture before the commencement of the study.

Each animal was weighed (live weight, LW) at the start and the end of the collection period of each of the experiments.

Environmental conditions within the building during Experiment 1 were not measured. However, outside air maximum and minimum temperatures (°C) and relative humidity (%) were measured daily throughout the study.

Forages and feeding management

Experiment 1: Fed indoors on lucerne hay

During Experiment 1 the animals were housed individually in digestibility crates placed 3 m from each other within a well-ventilated building. One side of the building was used for alpaca and the other for sheep. The alpaca were housed in crates of similar design to those described by Milne *et al.* (1978) for red deer, with internal dimensions of 1·72 m (length), 1·52 m (height) and 1·11 m (width). One side of the crate was movable, so the width was decreased to 0·75 m to prevent the alpaca from turning around. The sheep crates were of standard design. The design of the crates allowed automatic collection of faeces and urine from both species (Pinares-Patiño *et al.* 2003). Animals were fed *ad libitum* (allowing 10% refusal) on chaffed (~50 mm) lucerne hay. During the balance and forestomach sampling periods feeding level was fixed at 1·05 times the intake of each individual observed during the VFI measurement. The daily ration was fed at 08.00 h and drinking water was given *ad libitum*.

Experiment 2: Grazing on perennial ryegrass/white clover pasture (PRG/WC)

Two 0·4 ha paddocks (1 and 2) of PRG/WC pasture were selected for uniformity of herbage composition. Each paddock was subdivided into two plots (using a portable fence) and the animal species (alpaca or sheep) randomly allocated to the plots within one paddock. Thus, alpaca and sheep were grazed on paired plots as separate flocks. Within each plot, a fresh strip of pasture was grazed each day. Daily herbage allowance was controlled by electric fences (back and front) to offer 8 and 6 kg dry matter (DM) per head of alpaca and sheep, respectively. It was assumed that this level of allowance would maximize intake (Hodgson 1990).

Paddock 1 was grazed first, when the forage grasses were flowering. The whole of paddock 1 and one third of paddock 2 were grazed during the acclimatization of experimental animals, while measurements and sample collections were carried out while the animals were grazed in paddock 2, when the pasture was also in the flowering stage. During the animal measurements, herbage mass was 3490 ± 346 kg DM/ha, composed of perennnial ryegrass (75%), white clover (15%) and other species (10%; *Holcus lanatus*, *Agrostis capillaris*, etc.).

Experiment 3: Grazing on birdsfoot trefoil pasture (Lotus)

Two paddocks (0·4 ha each) of Lotus pasture were weeded manually with the aim of providing a pure stand of this pasture without the use of herbicides, residues of which might affect methanogenesis. The selected paddocks were in the late vegetative stage. There were weeds in either senescent (mostly grasses: perennial ryegrass and annual poa) or vegetative (mostly of the Compositae family) stages. The non-grass weeds were pulled out manually by their roots, but grasses were manually cut 5 cm above ground level. Weeding took place about 2 days before the animals were due to graze the strip.

After weeding, the total herbage mass was 5680 ± 437 kg DM/ha, of which 53, 42 and 5% were stems and green leaf of Lotus and senescent weeds (mostly stems of grasses), respectively. The subdivision of paddocks and grazing management were similar to that for the PRG/WC pasture (Experiment 2). However, because of the high proportion of stem material, daily pasture allowance was set up on the basis of leaf DM, rather than on whole plant DM.

Measurements and sample collection procedures

Experiment 1: Fed indoors on lucerne hay

The total amount of feed required for the whole of the 14-day data and sample collection period was estimated, prepared (chaffed) and after thorough mixing, duplicate samples were taken for DM determination (100 °C, 48 h). Another two samples were stored at −20 °C for chemical analysis. The amounts of feed refused were recorded daily and samples (50%) taken for daily DM determination (100 °C, 48 h). The remaining feed refusals were stored frozen (−20 °C). After the collection, all frozen samples were pooled within animals, mixed thoroughly and re-sampled, then freeze-dried, ground through a 1-mm mesh sieve (Wiley Mill, USA) and used for analyses.

During the energy and N balance measurement phase (6 days), samples (10%) of faeces were taken for daily DM determination (100 °C, 48 h). Other daily samples (10%) of the faeces were stored frozen (−20 °C) and later pooled within animals, mixed thoroughly, re-sampled, freeze-dried and ground (1-mm mesh sieve) for chemical analysis. Urine from both animal species was acidified at collection as described by Pinares-Patiño *et al.* (2003) and daily samples (10%) were diluted (1:3, v/v) in water, subsampled (20%) and stored (−20 °C) for later analysis of purine derivatives (PD) on samples pooled within each animal. Other samples (10%) of the daily urine production were taken, stored frozen and later pooled within animal, freeze-dried and analysed for energy and N contents.

Daily CH_4 production (g/day) was measured over days 7–10 by the sulphur hexafluoride (SF_6) tracer technique (Johnson *et al.* 1994*a*) following the procedures described by Pinares-Patiño *et al.* (2003).

Samples of forestomach contents (15–20 ml) were collected between 2·5 and 3·0 h post feeding on days 13 and 14 and this task took about 2 min per animal. Samples for protozoa counting were prepared using formal-saline solution and following the procedures described by Pinares-Patiño *et al.* (2003), but using whole (unstrained) forestomach contents. Samples of forestomach contents for VFA analysis were acidified, deproteinized and centrifuged immediately after sampling, using procedures described by Domingue *et al.* (1991).

Experiments 2 (grazing on PRG/WC) and 3 (grazing on Lotus)

Similar methods for collection of samples and their management were used in Experiments 2 and 3.

Samples of pasture on offer were obtained daily before animals entered the allocated pasture strips. Four (two for each animal species) 0·10 m^2 quadrats (0·40 × 0·25 m) were cut at ground level, weighed, pooled and subsampled for DM determination. Other daily samples of the pooled material were stored (−20 °C) for later within-period pooling, freeze drying, grinding (1-mm mesh) and chemical analysis.

For each animal species, samples of the grazed herbage were collected from within three 0·5 m^2 protected areas (using 1·0 × 0·5 m wire cages) by hand-cutting at the height to which animals had grazed outside the cages and imitating the selective grazing of sward components and plant parts. Daily samples were stored (−20 °C) and later pooled within animal species, freeze dried, ground and used for chemical analysis.

In both Experiments 2 and 3, daily CH_4 production (g/day) was measured over days 1–4 by the SF_6 tracer technique following the procedures described by Lassey *et al.* (1997). A minimum of 3 successful CH_4 sampling days was required from each animal.

Total faecal outputs by the grazing animals were collected twice daily using a harness and canvas bag. Collection of faeces was delayed by 1 day relative to the collection of samples for CH_4 measurement. Faeces from each animal were weighed, pooled within each day and sampled (10 %) for DM determination (100 °C, 48 h). Other subsamples (10 %) of the daily faeces output were stored (−20 °C) and later pooled within animal species, subsampled, freeze-dried, ground and used for chemical analysis.

Daily dry matter intakes (DMI) of each individual alpaca and sheep were estimated from the *in vitro* pasture dry matter digestibilities (DMD) in conjunction with the total faecal DM output by the individual animals.

On days 5 and 6, samples of forestomach contents were collected within 1 h after removal from grazing. Collection and management of samples for protozoa count and VFA analysis were carried out as for Experiment 1.

Laboratory methods

Samples of lucerne chaff (both offered and refused), pastures (both on offer and diets selected), faeces and urine were analysed for gross energy contents (GE, megajoules (MJ)/kg DM) using an adiabatic bomb calorimeter (Gallenkamp Autobomb; Loughborough, Leics, UK) and for total N by the Kjeldahl method. Organic matter (OM) content of lucerne hay, pasture samples, and faeces was determined by ashing in a furnace at 550 °C for 16 h, whereas their neutral detergent fibre (NDF) and acid detergent fibre (ADF) contents were determined according to the methods of Goering & van Soest (1970).

Samples of diet selected on PRG/WC and Lotus pastures were subjected to *in vitro* digestibility determinations by the enzymatic method of Roughan & Holland (1977), calibrated using either perennial ryegrass/white clover or birdsfoot trefoil standards with known *in vivo* digestibility values. Thus, digestibilities of DM (DMD) and OM (OMD) were determined.

Samples of the pastures (PRG/WC and Lotus) on offer and the diet selected were analysed for extractable and bound condensed tannins (CT) using the butanol-HCl procedure of Terrill *et al.* (1992*a*).

Urinary purine derivatives (PD), allantoin, xanthine (plus hypoxanthine) and uric acid were respectively determined using the colorimetric, enzymatic and uricase methods of Chen & Gomes (1992). PD excretion was used to estimate the microbial N supply from the forestomachs, according to the procedures described by Chen & Gomes (1992).

VFA concentrations in forestomach fluid were determined by gas chromatography (HRGC 5380, Carlo Erba Instruments, Italy) as described by Hoskin *et al.* (1995). The molar proportions (mol %) of acetate, propionate and butyrate, and the acetate/propionate (A/P) ratio were calculated. Management of formalin-treated forestomach fluid samples and protozoa counting were carried out as described by Pinares-Patiño *et al.* (2003). Protozoa counts were expressed per ml of forestomach contents.

Data calculation and statistical analysis

For Experiment 1, the VFI and apparent digestibilities of DM, OM, GE, ADF, NDF and N were determined from the measurements carried out during the VFI and balance periods in conjunction with the chemical composition of samples taken. In Experiments 2 and 3, these values were determined from the estimated DMI (based on *in vitro* DMD and faecal DM output) in conjunction with the chemical composition of samples taken. The daily VFI of DM (DMI), GE (GEI) and N (NI) were expressed per kg of $LW^{0.75}$.

Data for CH_4 emission were expressed in three ways: (1) on an absolute basis (per head, g/day), (2) the CH_4 energy loss as a percentage of the GEI (% GEI) and (3) the rate of CH_4 production per unit of digestible NDF intake (g/kg DNDFI). In this study, the terms 'CH_4 production', 'CH_4 yield' and 'CH_4 emission' are used as described by Pinares-Patiño *et al.* (2003).

In the present study, because the same animals were successively fed on three different forages, time and forage effects were confounded. It was thus not possible to test statistically the effects of forages and the interaction of forages and animal species. However, since the major objective of the study was to compare the two animal species (alpaca and sheep), data were analysed within each experiment (or forage) using Proc GLM of SAS (SAS 1985). Results are presented as the least squared means and standard error of means (±S.E.).

Hereafter, the three forages, lucerne hay, PRG/WC and Lotus, will be used in reference to Experiments 1, 2 and 3, respectively.

Table 1. *Chemical composition (g/kg DM) and apparent* in vitro *organic matter digestibility (OMD) of the forage on offer and of the diet selected by alpaca and sheep during lucerne hay feeding or grazing on perennial ryegrass/white clover pasture (PRG/WC) or birdsfoot trefoil pasture (Lotus)*

		Diet selected	
	Forage on offer	Alpaca	Sheep
Experiment 1: Fed indoors on lucerne hay			
Organic matter (OM)	909	912	909
Nitrogen (N)	36·5	36·7	38·3
Neutral detergent fibre (NDF)	384	394	380
Acid detergent fibre (ADF)	316	332	313
OM digestibility (OMD)	0·651	0·651*	0·650*
Experiment 2: Grazing on PRG/WC			
Organic matter (OM)	909	905	898
Nitrogen (N)	24	26	38
Neutral detergent fibre (NDF)	491	486	360
Acid detergent fibre (ADF)	300	303	242
Condensed tannins (CT)			
Extractable	0·52	0·62	0·536
Protein-bound	0·36	0·17	0·269
Fibre-bound	0·00	0·12	0·000
Total CT	0·88	0·91	0·805
OM digestibility (OMD)	0·720	0·677	0·766
Experiment 3: Grazing on Lotus			
Organic matter (OM)	926	921	919
Nitrogen (N)	28	32	43
Neutral detergent fibre (NDF)	422	380	249
Acid detergent fibre (ADF)	344	282	199
Condensed tannins (CT)			
Extractable	13·0	12·0	25·64
Protein-bound	10·6	9·8	17·01
Fibre-bound	1·8	1·7	0·94
Total CT	25·4	23·5	43·58
OM digestibility (OMD)	0·630	0·686	0·800

* *In vivo* mean OMD values ($n = 6$ animals).

RESULTS

Experiment 1: Fed indoors on lucerne hay

Diet quality, voluntary feed intake (VFI) and apparent digestibility of diet

The composition of the diet eaten by alpaca and sheep is given in Table 1. There were small differences, but statistical comparisons could not be made because only one pooled feed sample was analysed for each animal species.

Alpaca were much heavier ($P<0·01$) than sheep (63·3 *v.* 43·3 kg) (Table 2), but they ate significantly ($P<0·01$) less feed than sheep (Table 2). Comparatively (per kg $LW^{0·75}$), the mean feed intakes of sheep were about twice those of the alpaca.

There were no differences ($P>0·05$) between alpaca and sheep in their apparent digestibilities of DM (0·636 *v.* 0·639) or OM (0·651 *v.* 0·650), but alpaca were more efficient ($P<0·05$) than sheep in digesting both NDF (0·478 *v.* 0·461, s.e. $\pm$0·0057) and ADF (0·526 *v.* 0·503, s.e. $\pm$0·0058).

CH_4 emission, forestomach volatile fatty acid (VFA) proportions and protozoa counts

The CH_4 production (g/day) by alpaca was lower, but not significantly different ($P=0·12$) from that of sheep (Table 2). There was no difference ($P>0·05$) between the animal species in CH_4 yield (% GEI) or CH_4 production rates per kg DNDFI (Table 2).

The forestomach fluid of alpaca had higher ($P<0·01$) acetate/propionate ratio (A/P) than that of sheep, but the species did not differ ($P>0·05$) in butyrate concentrations (mol %) in their forestomach fluid (Table 2).

No holotrich protozoa were found in the forestomach contents of alpaca (Table 2), whereas holotrichs accounted for 1·0% of the total protozoa concentrations in the rumen contents of sheep. Sheep

Table 2. *Liveweight (LW), voluntary feed intake (VFI, per kg $LW^{0.75}$), CH_4 emission, forestomach volatile fatty acid (VFA) proportions and protozoa counts for alpaca and sheep fed indoors on lucerne hay in Experiment 1**

	Alpaca	Sheep	S.E. (D.F. = 10)
LW (kg)	63·3	43·3	3·61
VFI (per kg $LW^{0.75}$)			
DMI (g)	38·8	74·0	4·20
GEI (MJ)	0·74	1·36	0·077
NI (g)	1·4	2·7	0·15
CH_4 emission†			
g/day	14·9	18·8	1·70
% GEI	5·1	4·7	0·31
g/kg DNDFI	92·0	92·5	6·56
VFA			
Acetate/Propionate (A/P)	3·0	2·3	0·12
Butyrate (mol %)	6·9	6·5	0·66
Protozoa counts (10^5/ml)			
Holotrichs	0	0·04	0·020
Entodinomorphs	2·08	3·80	0·381
Total	2·08	3·84	0·381

* Abbreviations: DMI, GEI, NI, DNDFI, are intakes of dry matter, gross energy, nitrogen and digestible neutral detergent fibre, respectively.
† CH_4 emission expressed as: (1) CH_4 production (g/day), (2) CH_4 yield (% GEI), and (3) rate of CH_4 production per kg DNDFI.

Table 3. *Energy and nitrogen (N) balances, and microbial N supply from the forestomach for alpaca and sheep fed indoors on lucerne hay in Experiment 1*

	Alpaca	Sheep	S.E. (D.F. = 10)
Energy balance			
Intake (MJ/d)	16·0	22·0	1·40
Partition (% of intake)			
Faeces	37·3	38·1	0·36
Urine	5·2	5·8	0·13
Methane	5·1	4·7	0·31
Metabolizable	52·4	51·4	0·62
Nitrogen balance			
Intake g/day	31·2	45·1	2·81
Partition (% of intake)			
Faeces	25·3	25·2	0·37
Urine	57·4	57·8	2·52
Retained	17·2	17·0	2·70
Microbial N supply			
g/day	9·5	14·3	1·01
g/kg DOMR*	29·1	31·8	2·16

* DOMR, digestible organic matter apparently fermented in the rumen, estimated as 0·65 DOMI, digestible OM intake (Chen & Gomes 1992).

had significantly higher ($P<0·01$) counts (10^5/ml) of both entodinomorphs and total protozoa than alpaca.

Energy and nitrogen (N) balances and microbial N supply

The daily energy intake (GEI) by sheep (22·0 MJ/day) was significantly higher ($P<0·01$) than that of alpaca (16·0 MJ) (Table 3). Although the GEI loss as CH_4 did not differ between animal species (4·7 *v.* 5·1% GEI, for sheep and alpaca, respectively), the urinary energy loss was significantly ($P<0·01$) greater in sheep than in alpaca (Table 3).

The intake of nitrogen (N, g/day) by sheep was also significantly ($P<0·01$) higher than that of alpaca (Table 3), but there were no differences ($P>0·05$) in the N partitioning between urine and faeces between the animal species.

The daily microbial N supply was significantly ($P<0·01$) higher in sheep than in alpaca (14·3 *v.* 9·5 g/day) (Table 3). Nevertheless, when microbial N supply was expressed per kg of digestible OM apparently fermented in the rumen (DOMR), there were no differences ($P>0·05$) between the animal species.

Experiment 2: Grazing on perennial ryegrass/white clover pasture (PRG/WC)

Diet quality and voluntary feed intake (VFI)

The quality of the PRG/WC diet selected by alpaca was much lower than that selected by sheep (Table 1). For example, the N and NDF contents were lower and higher, respectively, in the diet of alpaca than in the diet of sheep. Accordingly, the OMD of the diet of sheep was higher than that of alpaca (Table 1). As expected the condensed tannin (CT) concentrations in the forage on offer and in the diets selected were low.

Alpaca were much heavier ($P<0·01$) than sheep (Table 4), but sheep had higher ($P<0·001$) VFI than alpaca (Table 4). For example, per kg $LW^{0.75}$ the GEI (MJ) and NI (g) of sheep were respectively 2·2 and 3 times higher than those of alpaca.

CH_4 emission, forestomach volatile fatty acid (VFA) proportions and protozoa counts

The CH_4 production (g/day) by alpaca was lower ($P<0·05$) than that of sheep (22·6 *v.* 31·1) (Table 4). However, the CH_4 yield (% GEI) of alpaca was higher ($P<0·05$) than that of sheep. No differences ($P>0·05$) between the species were found for the CH_4 production rates per kg DNDFI, A/P ratio or butyrate (mol %) (Table 4).

No holotrich protozoa were found in the forestomach contents of alpaca (Table 4), whereas in sheep holotrichs accounted for less than 1·0% of the total protozoa counts. Nevertheless, no differences

Table 4. *Liveweight (LW), voluntary feed intake (VFI, per kg $LW^{0.75}$), CH_4 emission, forestomach volatile fatty acid (VFA) proportions and protozoa counts for alpaca and sheep grazing on PRG/WC pasture in Experiment 2**

	Alpaca	Sheep	S.E. (D.F. = 10)
LW (kg)	65·1	46·4	3·23
VFI (per kg $LW^{0.75}$)			
DMI (g)	33·5	69·8	3·34
GEI (MJ)	0·61	1·32	0·063
NI (g)	0·9	2·7	0·12
CH_4 emission			
g/day	22·6	31·1	2·26
% GEI	9·4	7·5	0·81
g/kg DNDFI	95·2	103·1	10·17
VFA			
Acetate/propionate (A/P)	2·7	2·9	0·12
Butyrate (mol %)	12·0	11·0	0·74
Protozoa counts (10^5/ml)			
Holotrichs	0	0·04	0·020
Entodinomorphs	4·20	4·05	0·841
Total	4·20	4·09	0·843

* Abbreviations and CH_4 emission are the same as in Table 2.

Table 5. *Liveweight (LW), voluntary feed intake (VFI, per kg $LW^{0.75}$), CH_4 emission, forestomach volatile fatty acid (VFA) proportions and protozoa counts for alpaca and sheep grazing Lotus pasture in Experiment 3**

	Alpaca	Sheep	S.E. (D.F. = 10)
LW (kg)	63·2	47·2	3·17
VFI (per kg $LW^{0.75}$)			
DMI (g)	40·3	127·9	5·55
GEI (MJ)	0·77	2·53	0·109
NI (g)	1·3	5·5	0·23
CH_4 emission			
g/day	19·1	22·0	2·02
% GEI	6·4	2·7	0·26
g/kg DNDFI	152·0	70·0	6·47
VFA			
Acetate/propionate (A/P)	3·4	2·6	0·13
Butyrate (mol %)	11·6	13·7	0·74
Protozoa counts (10^5/ml)			
Holotrichs	0	0·12	0·039
Entodinomorphs	4·70	16·35	1·876
Total	4·70	16·47	1·873

* Abbreviations and CH_4 emission are the same as in Table 2.

($P > 0·05$) between the animal species were found in the total counts of protozoa in their forestomachs (Table 4).

Experiment 3: Grazing on birdsfoot trefoil pasture (Lotus)

Diet quality and voluntary feed intake (VFI)

As in the case of PRG/WC pasture, the quality of the Lotus diet eaten by alpaca was much lower than that eaten by sheep (lower N, but higher NDF contents) (Table 1). The OMD of the alpaca diet was much lower than that of sheep (0·686 *v.* 0·800) (Table 1). The concentration of CT in the diet selected by sheep was about twice that in the diet of alpaca or in the forage on offer (Table 1).

As expected, alpaca were heavier ($P < 0·01$) than sheep (Table 5). However, the VFI of sheep were much higher ($P < 0·001$) than those of alpaca (Table 5). For example, per kg of $LW^{0.75}$, the GEI (MJ) and NI (g) of sheep were 3·3 and 4·2 times higher, respectively than those of alpaca.

CH_4 emission, forestomach volatile fatty acid (VFA) proportions and protozoa counts

The CH_4 production (g/day) by alpaca was similar ($P > 0·05$) to that of sheep (19·1 *v.* 22·0). However, the CH_4 yield (% GEI) and the rate of CH_4 production per kg DNDFI were much higher ($P < 0·001$) for alpaca than sheep (Table 5).

There was a difference ($P < 0·001$) between the animal species in A/P ratio (3·4 *v.* 2·6; for alpaca and sheep, respectively), and the butyrate proportion (mol %) in the forestomach contents of sheep were slightly higher ($P = 0·07$) than those in alpaca (Table 5).

As observed in the other two forages (lucerne hay and PRG/WC), no holotrich protozoa were found in the forestomach contents of alpaca (Table 5) and holotrichs accounted for less than 1·0% of the total protozoa counts in sheep. Animal species significantly ($P < 0·001$) differed in their counts of entodinomorphs and total numbers of protozoa, with higher values for sheep (Table 5). The total concentration of protozoa (10^5/ml) in the forestomach of sheep was 3·5 times higher than that in alpaca (Table 5).

DISCUSSION

Diet selection

Within each of the three forages, the diet selected by the alpaca was of lower quality than that selected by sheep (Table 1). The higher OMD for sheep diets, especially under grazing conditions, might be attributed to the selection of particular plant parts (and plant species), which were higher in N but lower in fibre than the forage on offer. Even when fed on lucerne hay, sheep preferred the leafier material, whereas alpaca preferred the stalkier portions. This confirms the feeding preferences observed by Warmington *et al.* (1989) when llama × guanaco crosses and sheep were fed on ryegrass straw.

At grazing, the differences between species in diet selection were even greater. On PRG/WC, sheep selected mostly white clover and grass green leaf, whilst on Lotus, which was almost a pure stand, the sheep diet was composed almost entirely of Lotus leaves. In marked contrast, on PRG/WC, the alpaca avoided white clover but they grazed patches of pure grass completely to ground level. On Lotus, alpaca preferred primarily the senescent grass material (weeds), but because of the low availability of this material, Lotus stem and leaf materials were also eaten. The differences between species in selective grazing were very evident in this study and agree with the results from other studies with alpaca and sheep (Sharp *et al.* 1995) or guanacos and sheep (Bakker *et al.* 1997; Fraser & Gordon 1997; Fraser 1998).

Voluntary feed intake

On all the three forages, VFI was consistently lower ($P<0{\cdot}001$) in alpaca than in sheep (Tables 2, 4 and 5). This is consistent with a lower forestomach particulate FOR in alpaca (San Martin 1987).

The VFI of alpaca was relatively constant on all the three forages (38·8, 33·5 and 40·3 g DM/kg $LW^{0{\cdot}75}$, on lucerne hay, PRG/WC and Lotus, respectively) (Tables 2, 4 and 5). In contrast, the VFI of sheep was extraordinarily high when they were grazed on Lotus (128·0 g DM/kg $LW^{0{\cdot}75}$). Although it is expected that selective grazing under generous herbage allowance would yield highly digestible diets, the estimate of *in vitro* DMD of 0·787 for sheep grazing Lotus is slightly high compared with *in vivo* values in the literature (e.g. 0·766; Wang *et al.* 1994). Thus, the VFI of Lotus by sheep in the present study may have been overestimated because of the higher *in vitro* DMD used in the calculation.

Waghorn *et al.* (1997) and Barry & McNabb (2000) reported that forages containing more than 55 g CT per kg DM may depress VFI. However, Douglas *et al.* (1995) reported a CT concentration of 57·3 g/kg DM in the diet of sheep grazing Lotus, but the VFI of Lotus was greater ($P<0{\cdot}05$) than that of lucerne or Lotus × lucerne pastures. Similarly, Terrill *et al.* (1992*b*) reported that grazing sheep had higher ($P<0{\cdot}001$) DMI on sulla (*Hedysarum coronarium*; 36 g CT/kg diet DM) than on PRG/WC pasture (132 *v.* 90 g/kg $LW^{0{\cdot}75}$). The CT concentration in sheep diets determined in the present study was relatively low, 43·6 g/kg DM (Table 1). Thus, a depressing effect of CT in Lotus on VFI probably did not occur in this study.

The lowest intake recorded in the literature for alpaca was 28·8 g OM/kg $LW^{0{\cdot}75}$ for ryegrass hay (Reiner *et al.* 1987), but the animals lost weight. In the present study alpaca maintained their LW with an average OMI of 34 g/kg $LW^{0{\cdot}75}$, whereas sheep gained LW with an average OMI of 82·5 g/kg $LW^{0{\cdot}75}$.

CH_4 emission, forestomach volatile fatty acid (VFA) proportions and protozoa counts

Weather conditions showed little variation throughout this study and were unlikely to influence the CH_4 emission of the animal species. Mean (±S.D.) daily maximum and minimum temperatures (°C) and relative humidity (%) during Experiments 1, 2 and 3 were 18·2 (±2·55), 9·1 (±3·8) and 89·0 (±8·39); 19·8 (±2·94), 11·1 (±3·6) and 87·9 (±7·44); 19·1 (±2·23), 10·8 (±3·62) and 77·5 (±9·18), respectively.

Interpretation of the differences between animal species in CH_4 emission (Tables 2, 4 and 5) was complicated because these effects were confounded with those of the chemical composition of the diets eaten (Table 1) and VFI (Tables 2, 4 and 5).

Mean CH_4 productions (g/day) by sheep were within the range reported in the literature (Blaxter & Clapperton 1965; Pelchen & Peters 1998; Ulyatt *et al.* 1999). However, the CH_4 yields (% GEI) of sheep in this study were relatively lower than those reported in the literature (Pelchen & Peters 1998), which might be attributed to the effects of the *ad libitum* feeding (Blaxter & Clapperton 1965). In addition, the tracer technique used for CH_4 measurement, produces slightly lower CH_4 values (Johnson *et al.* 1994*b*; McCaughey *et al.* 1999), but relatively higher variation (Pinares-Patiño 2000) compared with indirect calorimetry. Similarly, the CH_4 yield of alpaca on lucerne hay (5·1%) (Table 2) was much lower than those (range 6·0–8·3%) reported for llamas fed on mixed diets (Schneider *et al.* 1974; Carmean *et al.* 1992). No other reports were found in the literature of CH_4 emission by SAC or from animals grazing on CT-containing forages.

On all the three forages the CH_4 production (g/day) by sheep were slightly higher (significant only on PRG/WC) than those by alpaca (Tables 2, 4 and 5). This can be attributed to the higher ($P<0{\cdot}001$) absolute DMI (per head, g/day) observed in sheep than in alpaca. On the other hand, except on lucerne hay (Table 2), the CH_4 yields (% GEI) were significantly lower ($P<0{\cdot}05$) in sheep than in alpaca. The latter is in agreement with the earlier findings by Blaxter & Clapperton (1965) that CH_4 yield decreases with increasing feed intake (relative to maintenance requirements) and with increasing diet digestibility.

Within animal species, GEI per kg $LW^{0{\cdot}75}$ on lucerne hay and PRG/WC was relatively similar (0·74 and 0·61 MJ for alpaca, and 1·36 and 1·32 MJ for sheep) (Tables 2 and 4). Despite that, the CH_4 yields

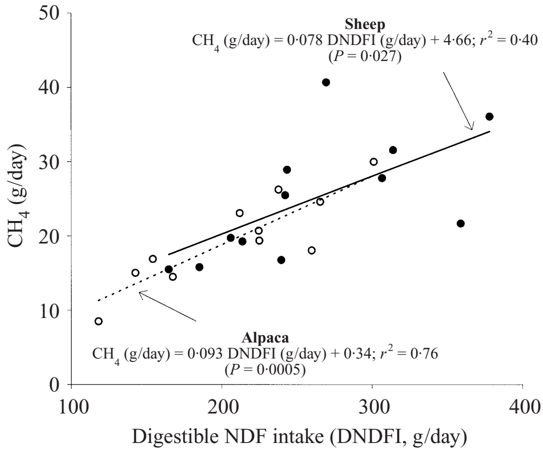

Fig. 1. Relationship between digestible neutral detergent fibre intake (DNDFI, g/day) and CH_4 production (g/day) for alpaca (○) and sheep (●), when data for lucerne hay and perennial ryegrass/white clover pasture (PRG/WC) were pooled within animal species.

(% GEI) of both animal species on PRG/WC were higher than those observed on lucerne hay (9·4 *v*. 5·1 in alpaca; 7·5 *v*. 4·7 in sheep) (Tables 2 and 4), but a positive relationship between the acetate/propionate (A/P) ratio in the forestomach fluid and CH_4 yield (Demeyer & van Nevel 1975) was not evident between these forages (Tables 2 and 4). On the other hand, in both animal species, the intakes of digestible NDF (DNDFI, g/day) on PRG/WC were higher ($P<0·001$) than those on lucerne hay (240·1 *v*. 161·5 in alpaca and 311·8 *v*. 208·7 in sheep; not tabulated). Thus, the higher CH_4 yields observed on PRG/WC (both in sheep and alpaca) may be attributed to the increased DNDFI, which is rich in the most methanogenic carbohydrates (cellulose and hemicellulose) (Moe & Tyrrell 1980).

The rate of CH_4 production per unit of DNDFI (g/kg DNDFI) did not differ ($P>0·05$) between animal species either on lucerne hay (Table 2), or PRG/WC (Table 4), which is in agreement with the concept that CH_4 production is mainly a function of cell wall digestion (Moe & Tyrrell 1980). In fact, when data for lucerne hay and PRG/WC were pooled within animal species, the only intake variable significantly related to CH_4 production (g/day) was DNDFI (g/day). The relationship between DNDFI and CH_4 production was stronger in alpaca ($r^2=0·76$) than in sheep ($r^2=0·40$) (Fig. 1), which suggests that the digestion of other feed constituents was also important for the CH_4 production in sheep. Nevertheless, neither gradients nor the intercepts of these regression lines were significantly different ($P>0·05$) from each other.

It has been documented (Fraser & Gordon 1997) that SAC strongly avoid dicotyledonous plants and it was observed in the present study that alpaca primarily ate dead and senescent material when grazed on Lotus pasture. Therefore, the lower NDF digestibility in alpaca on Lotus compared with that on lucerne hay (0·384 *v*. 0·478) may be attributed to the nature of the diet, rather than to any effect of CT on cellulolysis (Foley *et al.* 1999).

The depressed CH_4 yield (% GEI) by sheep on Lotus (2·7 %) agrees with earlier observations by Waghorn (1996), who found that sheep fed indoors on *Lotus pedunculatus* (80 g CT/kg DM) yielded less CH_4 than when fed on perennial ryegrass or lucerne pastures (3·9, 6·2 and 5·7 % GEI, respectively). Similar responses were also observed when dairy cows were fed silages of *Lotus pedunculatus* or perennial ryegrass (Woodward *et al.* 2001). In addition, other *in vitro* studies have also found depressing effects on CH_4 production of other CT-containing plant species such as *Mangifera indica* (Finger *et al.* 1998) and sainfoin (*Onobrychis viciifolia*) (McMahon *et al.* 1999).

The depressed CH_4 yield by sheep fed Lotus cannot entirely be attributed to the effects of their high intakes (Table 5) of high quality diets (Table 1) (Blaxter & Clapperton 1965), but probably also represents the action of some compound(s) in Lotus. It is recognized (Foley *et al.* 1999) that if tannins are present in a plant, then non-tannin phenolics are also present. Thus, whether CT or other compounds in Lotus contributed to the lower CH_4 yield observed in sheep remains to be determined, together with its mechanism of action.

The protozoal population in sheep grazing Lotus was four times higher than that on the other two forages, which is in agreement with similar observations when sheep were grazed on sulla (Terrill *et al.* 1992*b*). The reasons for the increased ciliate numbers on Lotus are not clear. Terrill *et al.* (1992*b*) suggested that the high contents of readily fermentable carbohydrates in sulla favoured protozoa growth, whereas CT did not have an adverse effect on it. The absence of holotrichs in the forestomach contents of camelids (Jouany 2000) is confirmed by the present study in alpaca (Tables 2, 4 and 5) and possibly it is due to the nature of their diets (poor in soluble carbohydrates) (Williams & Coleman 1992).

It is well documented (Jouany & Lassalas 2000) that, by virtue of inter-species H_2 transfer, more CH_4 is lost (% GEI) when protozoa are present in the rumen, and the larger the population of protozoa the greater is the effect. This relationship was confirmed by the present study for data within animal species, when lucerne hay or PRG/WC was fed (Tables 2 and 4). However, reasons for the increased protozoal population, but depressed CH_4 yield observed in sheep grazed on Lotus (Table 5) are unknown. Some compound in Lotus may have prevented the occurrence of the physical association between ciliates and methanogens necessary for the optimum transfer of H_2 (Ushida *et al.* 1997).

Feed digestibility, energy and N balances, and microbial N supply from the forestomachs in Experiment 1 (fed indoors on lucerne hay)

Compared with sheep, alpaca digested a significantly greater proportion of the feed NDF and ADF, which confirms the belief that SAC are more efficient in their ability to digest cell walls than sheep (San Martin & Bryant 1989; Lemosquet *et al.* 1996; Dulphy *et al.* 1997). The mechanism for this greater efficiency was attributed to the low fractional outflow rate (FOR) of feed particles from their forestomach (Lemosquet *et al.* 1996; Dulphy *et al.* 1997), which would also explain in part the lower VFI by alpaca observed in this and other studies with SAC (San Martin & Bryant 1989; Lemosquet *et al.* 1996).

When energy losses were partitioned, as a percentage of GEI (Table 3), there was no difference between the alpaca and sheep in the energy loss in CH_4, but alpaca had lower ($P < 0{\cdot}01$) losses of urinary energy than sheep. The availability of metabolizable energy (ME, % GEI) did not differ ($P = 0{\cdot}12$) between animal species (Table 3). Carmean *et al.* (1992) determined that llamas required 0·353 MJ ME/kg $LW^{0{\cdot}75}$ for maintenance, which is similar to the 0·392 MJ ME/kg $LW^{0{\cdot}75}$ eaten by the alpaca in the present study while they maintained their LW.

No differences were found between alpaca and sheep in partition of N (Table 3), which disagrees with previous findings that SAC are more efficient in conserving N (Warmington *et al.* 1989; Lemosquet *et al.* 1996; Dulphy *et al.* 1997). The latter is probably correct on low N diets, but not on diets high in N, such as lucerne hay.

In conclusion, observations in the current work are consistent with alpaca having a lower particulate FOR than the sheep: (1) the chemical compositions of diets selected were more fibrous in alpaca, requiring more time for digestion; (2) VFI was lower in alpaca, reflecting more time spent in the forestomach; and (3) digestibility of cell walls was higher in alpaca, a probable consequence of longer retention times in their forestomach. This, and the fact that alpaca and sheep differed in CH_4 yield (% GEI), suggest that differences between these species in particulate FOR from their forestomach might have been the underlying physiological mechanism responsible for the differences in CH_4 yield (Demeyer & van Nevel 1975; Okine *et al.* 1989; Pinares-Patiño *et al.* 2003). However, since VFI and diet quality also differed between animal species, it was impossible to determine the effect of animal species on CH_4 yield independently of the effects of differences in diet quality and intake. The low CH_4 yield observed on sheep grazing Lotus deserves further study in order to determine the reasons and mechanisms for that. Finally, the results of this study support the belief that SAC have adapted to the highly fluctuating supply of poor quality forages in the Andes by reducing their intake and decreasing the particulate FOR from their forestomach. Thus, compared with sheep, their higher ability to digest structural carbohydrates is associated with relatively higher CH_4 yield.

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Methane emission by alpaca and sheep fed on lucerne hay or grazed on pastures of perennial ryegrass/white clover or birdsfoot trefoil

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